Response to Anonymous Referee #1. We thank the anonymous reviewer for an insightful and thoughtful review. Below are our responses.

Referee 1: Are fluctuations in calculated CO2 caused by layer-specific differences in stomatal data or delta13C, or both? Are there significant differences in stomatal conductance or delta13C?

Author response: Indeed, in the traditional approach to atmospheric CO2 reconstructions using changes in plant physiology, inferred CO2 variations can be traced directly to either leaf carbon isotopic composition or changes in stomatal density. However, the approach that we try to advocate relies on gas-exchange modeling and it 1) is sensitive to any combination of changes in carbon isotopic composition and stomatal conductance, and 2) takes into account the cumulative response of different plant species (i.e. all the plant species determined from the plant fossil locality). This approach thereby accounts for the complexities that arise from non-linear, and even non-uniform physiological responses to changes in the climate, something that CO2 reconstructions using only stomata, or only leaf δ13C values, and only a single species cannot do. Moreover, as we note in the manuscript this comprehensive approach leads to a more accurate accounting of uncertainty in ultimate CO2 estimates than traditional approaches.

However, to address the reviewer’s question, we conducted ANOVA linked with TukeyHSD to test differences in leaf δ13C and Stomatal Density between zones. We approached the ANOVA – TukeyHSD with three different null hypotheses (H0): 1) leaf δ13C and stomatal density combining all species is the same for all zones, 2) leaf δ13C and stomatal density for all canopy species, after Z-score scaling of inter-species variation, is the same for all zones, and 3) leaf δ13C and stomatal density for the most abundant species, Litsea calicarioides, is the same for all zones. The p-value in all cases is higher than 0.05, indicating that H0 cannot be rejected in any of these scenarios, and that leaf δ13C and stomatal density do not individually change significantly between zones. Thus, variations in estimated CO2 are the result of the combination of leaf carbon isotopic composition, leaf conductance, and intra-species variation of physiological response to atmospheric carbon. The original carbon isotope and leaf conductance measurements are available in the supplementary material. We include new a section in the manuscript to further clarify how our approach means that a change in model output may be impossible to trace to a uniform change in input variables, and on a related note we emphasized the need for further evidence to further evaluate the role of a CO2 increase in driving Antarctic Ice melt at the Oligocene/Miocene boundary.

Referee 1: It would be also interesting to compare stomatal data of the fossil plants with those of their extant representatives. Are there significant differences?

Author response: We agree that this is an interesting research question, and it is currently considered in the context of a separate study. The comparison between fossil plants and their extant representatives is not of fundamental relevance to this manuscript and we prefer to keep it separate from the research results we are reporting here.

Referee 1: The treatment of intrinsic Water-Use Efficiency is too simplistic and should include consideration of the changes in fatty acid δD of the Foulden Maar record, in particular with regards to the influence of changes in humidity on plant water-use efficiency reconstructions.

Author response: We do have δD values and δ13C values from leaf waxes in this record that can provide some guidance for making inferences about changes in hydroclimate across the 100,000-yr period of sedimentation (Reichgelt et al., 2016). However, our discussion of iWUE is not meant to address variations that occurred during this interval, but instead focuses on contrasting the early Miocene values with modern values. To support our southern temperate reconstructed iWUE, we include results from the same transform functions on previously published records from Ethiopia and Panama, which showed
similar offsets from modern. That said, we agree with the referee that in a warmer world, whether you are
in the tropics or in the southern temperate region, you would expect higher vapor pressure deficits, which
would also drive up the iWUE signal. We have therefore expanded the discussion to address this
uncertainty and included Fig. S3 in the supplement to show that while temperatures Miocene New
Zealand are higher than modern, the relative humidity reconstructed for Foulden Maar is well within the
range of modern New Zealand forested biomes.

Referee 1: It is difficult to extrapolate leaf-level productivity to the canopy and vegetation level. It is
suggested that the authors mention and discuss the research on modern CO2 fertilization
experiments that highlight the complexity of physiological response in forests to increased
atmospheric carbon dioxide.

Author response: We expanded discussion on the confounding factors observed in modern CO2
fertilization experiments.

Referee 1: P. 2, l. 42 “will make more C available to the terrestrial biosphere”. This is an awkward
description of the anticipated fertilization effect of elevated CO2.

Author response: This sentence has been amended for clarity.

Referee 1: P. 4, l. 98 “For conductance measurements” This is not exactly correct. With fossil
leaves, anatomical data are determined which then allow to approximate conductance (on the basis
of various assumptions). This is not the same as measuring conductance of living leaves. P. 4, l. 103
See previous comment.

Author response: amended.

Referee 1: P. 8, ls. 194 – 195 There seems to be something wrong with the structure of this sentence.

Author response: amended.

Referee 1: P. 10, l. 229 - 231 “including a measure for the relative time the leaf is assimilating”.
What is the final value for this relative time? How was it determined? Additionally, the symbol for
this relative time appears to be the same as for the operational conductance.

Author response: amended.

Referee 1: P. 10, ls. 238 - 239 “is derived from Maire et al. (2015) which included coordinates, habit,
An and Gw data from which we could then calculate” It is not clear (from this sentence), how the
calculations were conducted in detail. Why were “coordinates” used and for what? Why where Gw
data from Maire et al. (and therefore of extant plants) used, and not conductance data derived from
stomatal data of the fossil plants?

Author response: amended.

Referee 1: P. 15, ls. 355 – 357 “In contrast to iWUE ... Gw for Miocene trees is similar to the
modern day range.” Since Gw is derived from Gc and therefore from fossil material, this would
mean that “structural” conductance is not that different for the fossil plants and their extant
relatives?
Author response: That is correct. We have expanded the discussion on this. We note (here and in the manuscript) that the extant relatives are not the same as the plants that currently occur at this latitude. Due to cooling the warm-temperate to subtropical diverse Lauraceae dominated rainforests of Miocene New Zealand no longer exist.

Referee 1: P. 15, ls. 357 - 359 “Increased atmospheric evaporative demand in combination with a longer growing season”. The authors describe that they used CLAMP to reconstruct growing season length. As far as I know, CLAMP provides also data on humidity. See also general comments.

Author response: Thanks for this excellent suggestion. CLAMP data on humidity have now been included in the supplementary material and are now included in our discussion.

Response to Referee #2, Gregory Retallack. Many thanks to Dr. Retallack for his insightful review. His comments are greatly appreciated.

Reviewer comment: This paper is well written and relatively free of errors, and presumably has been reviewed before.

Author response: It had not been reviewed before and we appreciate compliment.

Reviewer comment: Earth System Sensitivity (l.242) is a very slippery concept in this context, because the temperature increase with CO2 doubling in any one part of the world will depend on where it is. There are already numerous studies showing that midlatitude continental sites show little temperature change and thus muted sensitivity, but tropical and polar sites show marked changes in temperature. New Zealand is a temperate, site but also globally unusual in having a strongly marine-influenced climate now, and even more so in the Miocene when there was little land and few mountains. It is not clear how this even becomes relevant later (l.374) where elevated CO2 estimated is thought to relate to ESS of 4-7oC, because Miocene paleotemperature for New Zealand is not offered.

Author response: Perhaps this wasn’t clear enough in our discussion. We agree that local temperatures are not particularly instructive when considering ESS. The temperature change we considered was an estimate of the global average based on data and the transfer function approach presented in Hansen et al. (2013). We have updated the text to clarify this. While this approach itself has its limitations (which we also discuss in the manuscript), we believe that it is a reasonable basis for the ESS discussion and that this discussion is valuable.

Reviewer comment: I fail to see the relevance of C4 grassland expansion (l. 388) because it postdated the age of these New Zealand leaves by some 10 million years.

Author response: We updated the text to better explain the relevance of C4 grassland expansion in the late Miocene in the context of our results.

Reviewer comment: Errors in estimated paleoatmospheric CO2 are asymmetric and very large (l. 307-8). Perhaps this is due to inadequate numbers of stomates counted: it should be hundreds in each image. Furthermore, Gaussian error propagation can be used to calculate symmetrical errors. Both issues are addressed in the following paper too recent to be included - Retallack, G.J. and

Author response: The reviewer raises an interesting point about the numbers of stomata per image counted resulting in larger error bars. We have now added text to further clarify how we avoided systematic error propagation and we now have referenced the reviewer’s suggested study to highlight the importance of the number of counts per image.

The asymmetrical error propagation is the result of the gas-exchange model iteratively solving for conductance, assimilation rate and carbon dioxide, centered around a representative assimilation rate ($A_0$) measured under modern day atmospheric carbon dioxide. Because of this approach, the model returns a greater number of divergent solutions for fossil conductance, assimilation rate, and carbon dioxide for high CO2 estimates, and fewer for low CO2 estimates.
Elevated CO₂, increased leaf-level productivity and water-use efficiency during the early Miocene

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Abstract. Rising atmospheric CO₂ is expected to increase global temperatures, plant water-use efficiency, and carbon storage in the terrestrial biosphere. A CO₂ fertilization effect on terrestrial vegetation is predicted to cause global greening as the potential ecospace for forests expands. However, leaf-level fertilization effects, such as increased productivity and water-use efficiency, have not been documented from fossil leaves in periods of heightened atmospheric CO₂. Here, we use leaf gas-exchange modeling on a well-preserved fossil flora from early Miocene New Zealand, as well as two previously published tropical floras from the same time period, to reconstruct atmospheric CO₂, leaf-level productivity, and intrinsic water-use efficiency. Leaf gas-exchange rates reconstructed from early Miocene fossils which grew at southern temperate and tropical latitudes, when global average temperatures were 5–6°C higher than today reveal that atmospheric CO₂ was ~450–550 ppm. Early Miocene CO₂ was similar to projected values for 2040AD, and is consistent with Earth System Sensitivity of 3–7°C to a doubling of CO₂. The
Southern Hemisphere temperate leaves had higher reconstructed productivity than modern analogs likely
due to a longer growing season. This higher productivity was presumably mirrored at northern temperate
latitudes as well, where a greater availability of landmass would have led to increased carbon storage in
forest biomass relative to today. Intrinsic water-use efficiency of both temperate and tropical forest trees
was high, toward the upper limit of the range for modern trees, which likely expanded the habitable range
in regions that could not support forests with high moisture demands under lower atmospheric CO₂.
Overall, early Miocene elevated atmospheric CO₂ sustained globally higher temperatures and our results
provide the first empirical evidence of concomitant enhanced intrinsic water-use efficiency, indicating a
forest fertilization effect.

1 Introduction

Terrestrial plants comprise 450 Gt of carbon, representing 80% of Earth’s dry carbon (C) biomass (Bar-on
et al., 2018). Globally, plants draw down ~120 Gt of atmospheric C per year through photosynthesis,
representing the largest annual C flux on Earth (Beer et al., 2010). Total plant biomass is believed to be
determined in large part by atmospheric carbon dioxide concentrations (Cₐ), and it is predicted that future
increases in Cₐ will have a three-pronged effect on the terrestrial biosphere: 1) increased global
temperatures will shift the boundaries of climate zones and thereby the potential forest expanse (Rubel
and Kottek, 2010); 2) productivity will increase because global photosynthesis is C limited and increased
Cₐ will have a fertilization effect on the terrestrial biosphere (Zhu et al., 2016); and 3) elevated Cₐ will
increase plant water-use efficiency and reduce the threshold for physiological drought (Cernusak, 2020),
making more land area available for biosphere expansion (Zhou et al., 2017). Plant fossils record the
effect of past changes in climate, including CO₂ enrichment, and thus fossil floras provide insight into
changes in the carbon cycle and their effects on the terrestrial biosphere from a natural, whole-ecosystem
perspective.

The Miocene has been considered problematic for our understanding of Earth System Sensitivity
(ESS) to Cₐ, because most proxy-based Cₐ estimates indicate concentrations near 300 ppm (Foster et al.,
close to pre-industrial values, yet global temperatures were 5–6 °C higher than modern (Hansen et al., 2013). Enhanced radiative forcing is required to maintain such elevated early Miocene temperatures (Herold et al., 2010; Hansen et al., 2013), and without elevated Ca, climate models cannot achieve such high global temperatures in the Miocene (Henrot et al., 2010). The early Miocene also had an expanded biosphere compared to today, including woody vegetation in locations that are currently too cold and/or too dry for forests (e.g. Askin and Raine, 2000; Herold et al., 2010). A biosphere of the magnitude observed in the early Miocene fossil record requires elevated temperatures and plant water-use efficiency, suggesting Ca levels higher than estimated by most existing proxy reconstructions (Herold et al., 2010; Henrot et al., 2010). Importantly, plant-based Ca reconstructions have challenged the consensus of low Ca in the early Miocene (Kürschner and Kvaček, 2009; Reichgelt et al., 2016; Tesfamichael et al., 2017; Londoño et al., 2018) and previous interpretations of alkenone-based Ca proxies are being disputed (Bolton et al., 2016; Witkowski et al., 2019).

We applied plant gas-exchange modeling (Franks et al., 2014) to fossil leaves from the early Miocene (~23 Ma) rainforest ecosystem from southern New Zealand preserved in the Foulden Maar deposit (Bannister et al., 2012; Reichgelt et al., 2013; Conran et al., 2014; Lee et al., 2016) to reconstruct carbon assimilation rates ($A_n$), intrinsic water-use efficiency ($iWUE$; the ratio between carbon assimilation and stomatal conductance to water), and the Ca levels required to maintain these values. The same analyses were performed on previously published leaf $\delta^{13}$C and micromorphological measurements from two early Miocene fossil floras from Ethiopia (Tesfamichael et al., 2017) and Panama (Londoño et al., 2018). These two studies were incorporated here because they represent a similar time period (early Miocene) and the authors applied the same gas-exchange methodology. Because $A_n$, $iWUE$, and Ca are interdependent (Farquhar et al., 1980; Drake et al., 1997), we reconstructed these variables in concert for each fossilized leaf recovered from these forest ecosystems. This allows us to make inferences concerning carbon availability, productivity, and water balance in the forest.

2 Methods
2.1 Site Description

Foulden Maar (Fig. 1a) is a unique Konservat-Lagerstätte with abundantly preserved plants and insects (Kaulfuss et al., 2015; Lee et al., 2016) in southern New Zealand (45.527°S, 170.219°E). It was formed in an ancient maar-diatreme lake (Fig. 1b) at the Oligocene/Miocene boundary (Fox et al., 2015; Kaulfuss, 2017) and consists of ~100 kyr of annually laminated diatomite (Lindqvist and Lee, 2009; Fox et al., 2016). The Foulden maar-diatreme complex is part of the larger late Oligocene – late Miocene Waipiata Volcanic Field that produced a variety of maar volcanoes and scoria cones (Németh and White, 2003). Plant fossils used in this study were collected from a ~183 m long drill core (Fig. 1c). The Lauraceae-dominated rainforest (Bannister et al., 2012) surrounding the lake grew at a paleolatitude of ~50°S (Fig. 1a). The climate was marginally subtropical with a mean annual temperature of ~18°C, similar to modern day climates at 30°S (Reichgelt et al., 2019). The length of the growing season in this climate was ~10 months, compared to 5–6 months today, as reconstructed from the surface exposure macrofossil assemblage using the Climate Leaf Analysis Multivariate Program (Reichgelt et al., 2013).

2.2 Fossil leaf anatomy and paleoecology

Mummified fossil leaves were extracted from turbidite deposits that occur frequently within the Foulden Maar diatomite core (Fox et al., 2015). The diatomite is loosely consolidated allowing mummified leaves to be extracted using a combination of water and scalpels. After extraction, the leaves were cut into three pieces: one for bulk δ13C analysis, one for stomatal conductance measurements, and a third as a reference specimen. Leaf δ13C was measured using a Costech elemental combustion system (EA) coupled to a Delta V Plus IRMS (Thermo). In order to place measured δ13C on the VPDB scale, we calibrated measurements using a two-point isotope calibration based on the USGS40 and USGS41 standards. Measurement uncertainty was calculated by replicating ~15 samples two or three times and applying averaged uncertainty to the remaining leaves. For stomatal density and geometry measurements the leaves were soaked in hydrogen peroxide (H2O2) with up to 40% dilution, with tetra-sodium pyrophosphate salt crystals (Na4P2O7·10[H2O]), on a boiling plate at 40–50 °C for 1–2 hours (Bannister et al., 2012). When
the adaxial and abaxial cuticle layer could be separated, the leaf layers were cleaned of mesophyll cell
debris using small paintbrushes and both layers were stained with <0.5% Crystal Violet (C$_{25}$N$_3$H$_{30}$Cl) and
mounted on glass slides with glycerin jelly. Stomatal conductance and geometry measurements were
made on pictures at 100× magnification using TSView 7.1.1.2 microscope imaging software on a Nikon
Optiphot. Leaves were often fragmented and the cuticle wrinkled because the leaves were deposited in
turbidites. Moreover, there was strong divergence in overall cell and stomatal density, because we made
measurements on all species recovered from the sediments. To avoid systematic errors arising from
wrinkled cuticle, differing leaf architecture between species, or low cell counts (Retallack and Conde,
2020), each picture was given a standard bounding box (0.3 × 0.3 mm) on which cells were counted, to
calculate stomatal density. The number of cells in each bounding box ranged from 100 – 750, strongly
dependent on species. Five to eight pictures were taken of each leaf to constrain errors in cell density.
Stomatal size measurements were made using ImageJ 1.48v software (Schneider et al., 2012).

18 distinct leaf morphotypes were identified from the Foulden Maar drill core. Descriptions and
justification for identification are found in the Supplementary Information. Species identifications are
provided, where possible, based on paleobotanical studies from the Foulden Maar surface exposures.
Known species recovered from the Foulden Maar drill core are *Litsea calicarioides* (Fig. S1a),
*Cryptocarya taieriensis* (Fig. S1b), *C. maarensis* (Fig. S1i), *Beilschmiedia otagoensis* (Fig. S2a)
(Lauraceae) (Bannister et al., 2012), *Laurelia otagoensis* (Fig. S2h) (Atherospermataceae) (Conran et al.,
2013), and *Hedycarya pluvisilva* (Fig. S2i) (Monimiaceae) (Conran et al., 2016). Otherwise, tentative
genus or family identifications are provided, or unspecified morphotypic qualifiers, for leaves that could
not be assigned a plant group. These will henceforth be referred to as “C” (Fig. S1c), cf. *Myrtaceae* (Fig.
S1d), cf. *Ripogonum* (Fig. S1e), cf. *Myrsine* (Fig. S1f), “H” (Fig. S1g), cf. *Elaeocarpaceae/Cunoniaceae*
(Fig. S1h), cf. *Dysoxylum* (Fig. S2b), cf. *Cryptocarya* (Fig. S2c), “O” (Fig. S2d), “P” (Fig. S2e), “Q”
(Fig. S2f) and cf. *Endiandra* (Fig. S2g).

We made 375 anatomical and 80 carbon isotope measurements on 72 organically preserved fossil
leaves representing the 18 species collected from the Foulden Maar deposit (Fig. 1a). The affinities of
modern living relatives of the plant types at Foulden Maar strongly suggest that during the Miocene the site was characterized by a multi-layered closed canopy rainforest ecosystem (Reichgelt et al., 2013; Conran et al., 2014). In order to determine atmospheric carbon (Ca), intrinsic water-use efficiency (iWUE), and carbon assimilation rates (A_n), the ecological strategies of the individual fossil species at Foulden Maar need to first be established (Reichgelt and D’Andrea, 2019). Understory species rarely experience light saturation and utilize respired CO_2 that has already undergone isotopic fractionation; both conditions influence gas-exchange modelling results (Royer et al., 2019). Therefore, Ca reconstructed from understory species cannot be considered indicative of true global Ca. Here, we determine whether a fossil leaf type was likely in the canopy or the understory, based on 1) leaf δ^{13}C, 2) leaf cell density, and 3) sinuosity of the epidermal cell walls. A large range of leaf δ^{13}C in a single species is indicative of different levels of light saturation, which indicates that this species may preferentially occur in the subcanopy or in the understory (Graham et al., 2014). Leaves in the canopy, experiencing light saturation, divide epidermal cells rapidly compared to leaves in the shade, leading to high cell densities and relatively high leaf mass per areas in sun-exposed leaves (Šantrůček et al., 2014). Finally, a high level of anticlinal cell wall sinuosity has been interpreted as indicative of low-light conditions (Kürschner, 1997; Bush et al., 2017). We consider these three lines of evidence occurring in concert as indicative of a canopy or subcanopy ecological preference.

2.3 Modelling gas-exchange

Atmospheric carbon dioxide (C_a), plant photosynthesis (A_n), and intrinsic water-use efficiency (iWUE) are tightly linked (Farquhar et al., 1980; Drake et al., 1997), which allows us to solve for these parameters iteratively, through anatomical and carbon isotope (δ^{13}C) measurements of the fossil leaves. The Franks et al. (2014) gas-exchange model solves for C_a by iteratively reconstructing A_n and leaf conductance to atmospheric carbon (G_c), using a Monte Carlo approach. This means that every C_a reconstruction has an associated A_n and G_c value.
\[ C_a = \frac{A_n}{G_c \times \left( 1 - \frac{C_i}{C_a} \right)} \]  

(1)

In which \( C_i / C_a \) represents the ratio of intercellular carbon to atmospheric carbon, which can be reconstructed using known leaf fractionation processes: fractionation caused by diffusion (a), carboxylation (b), and fractionation caused by the preferential uptake of \(^{12}\)C to \(^{13}\)C in photosynthesis (\( \Delta \)), which is also influenced by the rate at which the leaf is photosynthesizing (Farquhar et al., 1982).

\[ \frac{C_i}{C_a} = \Delta - a \frac{b - a}{b} \]  

(2)

Here, \( a = 4.4\% \) and \( b = 29\% \) (Farquhar et al., 1982; Roeske and O’Leary, 1984). \( \Delta \) can be calculated from the \( \delta^{13}\)C of the air, derived from Tipple et al. (2010) and measurements of leaf \( \delta^{13}\)C (Farquhar and Richards, 1984; Farquhar et al., 1989). Leaf and air \( \delta^{13}\)C used in the Franks et al. (2014) model are presented in Table S1.

\[ \Delta = \frac{\delta^{13}C_{air} - \delta^{13}C_{leaf}}{1 + \delta^{13}C_{leaf}} \]  

(3)

\( G_c \) is determined by the maximum capacity for conductance of a leaf surface (\( G_{max} \)), the ratio of operational conductance to \( G_{max} \) (\( \zeta \)), boundary layer conductance (\( G_b \)), and mesophyll conductance (\( G_m \)) (Franks et al., 2014).

\[ G_c = \left( \frac{1}{G_b} + \frac{1}{\zeta \times G_{max}} + \frac{1}{G_m} \right)^{-1} \]  

(4)
$G_b$, $\zeta$, and $G_m$ are all changeable under natural conditions (e.g. Schuepp, 1993; Niinemets et al., 2009; Londoño et al., 2018) and it is highly disputed if these variables can be determined from fossil leaf material at all (e.g. McElwain et al., 2016; Soh et al., 2017). However, we adopt a standardized approach put forward by Franks et al. (2014) to obtain input for these variables. $G_b = 2 \pm 0.1 \text{ mol m}^{-2} \text{ s}^{-1}$, $\zeta = 0.2 \pm 0.02$ (Franks et al., 2009; Dow et al., 2014), and $G_m$ is determined using an empirical calibration (Evans and Von Caemmerer, 1996).

\[ G_m = 0.013 \times A_n \] (5)

$G_{\text{max}}$ is determined using predominantly measurable anatomical features of the fossil leaf cuticle (Franks and Beerling, 2009): stomatal density (SD), maximum aperture surface area ($a_{\text{max}}$), pore depth ($p_d$), and the ratio of diffusivity of CO2 in air over the molar volume of air ($d/v$), here taken as 0.000714 mol m$^{-1}$ s$^{-1}$ (Marrero and Mason, 1972).

\[ G_{\text{max}} = \frac{d/v \times SD \times a_{\text{max}}}{p_d + \pi \sqrt{a_{\text{max}}/\pi}} \] (6)

In this equation, SD can be measured directly from the leaf, $p_d$ is assumed to be the same as guard cell width (gcw), and $a_{\text{max}}$ is determined assuming a circular opening for the aperture, with the measurable pore length ($p_l$) as the diameter (Franks et al., 2014).

\[ a_{\text{max}} = \pi \times \frac{p_l}{4} \] (7)

Measurements of SD, gcw and $p_l$ used in the Franks et al. (2014) gas-exchange model are presented in Table S1.
Because $A_n$ is required to solve $G_m$, $G_c$ is solved iteratively, though $G_c$ is largely determined by measurable anatomical parameters. However, $A_n$ is also solved iteratively, as it is dependent on $C_a$ and the carbon saturation value ($\Gamma$), set at 40 ppm (Franks et al., 2013).

$$A_n \approx A_0 \times \frac{(C_a - \Gamma) \times (C_{a0} + 2\Gamma)}{(C_a + 2\Gamma) \times (C_{a0} - \Gamma)} \quad (8)$$

In which $A_0$ is the photosynthetic rate of a modern model species that can represent the fossil species’ photosynthetic rate, and $C_{a0}$ is the atmospheric carbon dioxide level at which $A_0$ was measured. $A_0$ for each fossil species was derived from the compilation of photosynthetic rates presented in Reichgelt and D’Andrea (2019). For fossil leaves with known modern relatives, we constrained the possible $A_0$ range by only including modern relatives within the same family or order, i.e. Lauraceae for Litsea calicarioides, Cryptocarya taieriensis, C. maarensis, cf. Cryptocarya, Beilschmiedia otagoensis and cf. Endiandra, Myrtaceae for cf. Myrtales, Liliales for cf. Ripogonum, Primulaceae for cf. Myrsine, Elaeocarpaceae and Cunoniaceae for cf. Elaeocarpaceae/Cunoniaceae, Meliaceae for cf. Meliaceae, Atherospermataceae for Laurelia otagoensis, and Laurales for Hedycarya pluvialis. Then, following the method of constraining $A_0$ of modern living relatives presented in Reichgelt and D’Andrea (2019), only $A_0$ values of plants with similar growth forms to the fossil plants, and growing in similar light environments as Foulden Maar were included. $A_0$ and $C_{a0}$ used in the Franks et al. (2014) model, and associated ecology of fossil leaf types is shown in Table S2.

The Franks et al. (2014) gas-exchange model thus iteratively solves for $C_a$, $A_n$, and $G_c$. However, only leaves derived from canopy trees are likely to represent these values at light saturation. Moreover, plants in the understory assimilate a mix of atmospheric and respired CO$_2$, which has therefore already undergone fractionation processes, making the calculated $C_i/C_a$ problematic. Therefore, we present the
results for $C_a$, $A_n$, and $G_c$ of leaf types most likely to be derived from canopy trees separately, as they are more likely to not have a systematic skew.

$iWUE$ is defined as the ratio between $A_n$ and stomatal conductance to water (Feng, 1999).

\[
iWUE = \frac{A_n}{G_w} \tag{9}\]

Due to the different rates at which carbon dioxide and water vapor diffuse in air, a transformation of $G_c$ is required to calculate $G_w$.

\[
G_w = 1.6 \times G_c \tag{10}\]

Finally, cumulative annual carbon uptake through photosynthesis ($A_{tot}$) can be calculated in gC m$^{-2}$ yr$^{-1}$, by transferring from moles to grams, including a measure for the relative time the leaf is assimilating carbon ($\zeta$), and the length of the growing season.

\[
A_{tot} = (2.6 \times \zeta \times A_n \times t_g) \times 12 \tag{11}\]

In which $t_g$ is the length of the growing season in months, which we can derive from the fossil plant assemblage (Reichgelt et al., 2019), using the method of Spicer et al. (2009). $G_w$, $A_{tot}$, and $iWUE$ values for $Litsea calicarioides$, $Cryptocarya taieriensis$, $C. maarensis$, cf. Elaeocarpaceae/Cunoniaceae, and cf. Myrtaceae are presented in Table S3. The modern reference $A_n$ and $G_w$ data are derived from Maire et al. (2015), which, using transform functions 9 and 11, we also used to calculate $iWUE$ and $A_{tot}$.

2.4 Comparison to Earth System Sensitivity
Earth System Sensitivity to Ca (ESS) is the amount of temperature increase expected under a doubling of atmospheric CO2. This sensitivity is likely not static in Earth’s history and is dependent on, among other aspects, continental configuration and ocean circulation patterns (Royer, 2016). Here, we estimate global surface temperature for the early Miocene following the approach of Hansen et al. (2013). We then use these temperature estimates along with a broad range of commonly cited Neogene ESS, of 3–7°C (Hansen et al., 2013; Royer, 2016), to provide a model for the expected early Miocene Ca. Following this model, ultimately means that a doubling of Ca compared to pre-industrial levels is expected when an increase of global average surface temperatures (Ts) of 3–7°C compared to modern occurs.

Compiled deep-sea benthic foraminifera δ18O data of the last 30 million years (Zachos et al., 2001) were averaged into 20 kyr time bins. Deep-sea temperatures (Td) were then calculated using the linear transfer functions of Hansen et al. (2013), which depend on the presence of sea-ice.

\[
T_d = 5 - 8 \times \frac{\delta^{18}O - 1.75}{3} \text{ IF } (\delta^{18}O < 3.25) \tag{12}
\]

\[
T_d = 1 - 4.4 \times \frac{\delta^{18}O - 3.25}{3} \text{ IF } (\delta^{18}O > 3.25) \tag{13}
\]

Ts was then calculated for post-Pliocene using:

\[
T_s = 2 \times T_d + 12.25 \tag{14}
\]

For the Pliocene:

\[
T_s = 2.5 \times T_d + 12.15 \tag{15}
\]

And for pre-Pliocene we assumed that Ts changed linearly with Td, by a factor of 1.5.

\[
\Delta T_s = 1.5 \times \Delta T_d \tag{16}
\]
C\textsubscript{a} based on an ESS range of 3–7°C was then calculated using the resulting \( T\_s \).

\[
C\textsubscript{a} = 310 \times \frac{T\_s\[x\] - T\_s\[0\]}{2 \times \text{ESS}} + 310 \quad (17)
\]

In which \( T\_s\[x\] \) is the calculated average global surface temperature at time \( x \), \( T\_s\[0\] \) is the modern day average global surface temperature, and 310 represents pre-industrial \( C\textsubscript{a} \).

3 Results and Discussion

3.1 Southern Temperate Rainforest Paleoecology

Modern day Lauraceae rainforests in New Zealand have a single dominant canopy tree, \textit{Beilschmiedia tawa}, and its farthest southern extent is ~42°S (Leathwick, 2001), which is the farthest southern occurrence of any arborescent Lauraceae species in the world. Rainforests further south in New Zealand are usually dominated by Nothofagaceae or Podocarpaceae, and the only modern-day forests at ~50°S are the Magellanic Subpolar Forests in southern South America. Low-growing Podocarpaceae/Nothofagaceae forests, similar to modern forests in southern New Zealand and southern South America, dominated Antarctic vegetation during the early Miocene (Askin and Raine, 2000) and the Foulden Maar rainforest included at least ten Lauraceae species (Bannister et al., 2012), emphasizing the expanded biosphere potential in the early Miocene compared to today (Herold et al., 2010).

We identify \textit{Litsea calicarioides}, \textit{Cryptocarya maarensis}, \textit{C. taieriensis}, cf. Elaeocarpaceae/Cunoniaceae, and cf. Myrtaceae as the most probable canopy components because they lack characteristics typical of understory components, 1) the large range of leaf \( \delta^{13}C \) values and relatively low overall leaf \( \delta^{13}C \) values (Graham et al., 2014), 2) low cell densities (Kürschner, 1997; Bush et al., 2017) (Fig. 2 a,b), and 3) the undulating or sinuous cell walls (Kürschner, 1997; Bush et al., 2017).

Modern day \textit{Litsea calicaris} in New Zealand is also part of the canopy, though rarely dominant (de
Lange, 2020), whereas Cryptocarya is extinct in New Zealand. Members of Elaeocarpaceae, Cunoniaceae
and Myrtaceae in modern day New Zealand, such as Weinmannia racemosa (Cunoniaceae) and
Metrosideros robusta (Myrtaceae) can attain heights of over 25 meters (de Lange, 2020).

The most likely subcanopy or understory taxa were cf. Ripogonum, cf. Myrside, “O”, and cf.

Dysoxylum, because leaf fossils of these types have both low leaf $\delta^{13}C$ and sinuous or undulating cells
(Fig. S1e,f, S2b,d). Ripogonum scandens in modern day New Zealand is a twining forest liana, often
found in the understory, Myrside comprises several species of shrubs and small trees; whereas Dysoxylum
spectabile in modern day New Zealand is a medium-sized tree (de Lange, 2020). The affinity of

morphotype “O” is unclear, but likely represents a now extinct plant group in New Zealand. Hedycarya.

“P”, and “Q”, all displayed some variation in these features and occurred in relatively low abundance, and
are therefore considered of uncertain ecological affinity.

3.2 Earliest Miocene CO$_2$

Gas-exchange modeling (Franks et al., 2014) of canopy leaves throughout the Foulden Maar core
indicates that C$_a$ (+1σ) was 445 +618 / -100 ppm, whereas reconstructed C$_a$ from understory elements
yields C$_a$ of 622 +3017 / -161 ppm (Fig. 2c), consistent with understory plants assimilating respired CO$_2$
that has undergone prior fractionation processes, as well as experiencing elevated levels of C$_a$ under the

canopy (Graham et al., 2014; Royer et al., 2017). Prior work on the Foulden Maar core established three
different phases based on bulk organic $\delta^{13}C$ (Fig. 1c), fatty acid $\delta^{13}C$, and fatty acid $\delta D$: Phase I (80–105
m depth) with high $\delta^{13}C$ and low $\delta D$, Phase II (55–65 m depth) with low $\delta^{13}C$ and high $\delta D$, and Phase III
(0–45 m depth) with high $\delta^{13}C$ and low $\delta D$ (Reichgelt et al., 2016). Phase III can be further subdivided
into Phase IIIa (30–45 m depth) and IIIb (0–20 m depth), as Phase IIIa exhibits a period of low fatty acid
$\delta^{13}C$ and high $\delta D$, which is not expressed in bulk organic $\delta^{13}C$ (Reichgelt et al., 2016). Gas-exchange
modelling on leaves from these phases (Fig. 1c) suggest that during Phase II and IIIa C$_a$ may have been
elevated (C$_a$ = 529 +1159 / -125 and C$_a$ = 538 +769 / -181 ppm, respectively) compared to Phase I and
Phase IIIb ($C_a = 444 \pm 572 / -95$ and $442 \pm 1219 / -110$ ppm, respectively) (Fig. 3). Although gas-exchange modeling input reconstructed differing $C_a$ between phases, differences in overall conductance parameters, such as stomatal density and leaf $\delta^{13}C$, are not apparent (Table S1), despite differences in bulk $\delta^{13}C$, fatty acid $\delta^{13}C$, and $\delta D$ (Reichgelt et al., 2016). This is likely the result of non-uniform species responses to environmental changes in a complex multi-layered rainforest ecosystem, such as at Foulden Maar.

The advantage of using gas-exchange modeling to reconstruct $C_a$ from multiple species is that the uncertainty is quantified and constrained, greatly reducing the potential for systematic error in the final estimate (Reichgelt and D’Andrea, 2019; Royer et al., 2019). Along with the enhanced accuracy comes a more comprehensive appraisal of uncertainty than is achieved using other proxy approaches (Fig. 4).

Proxy error propagation is based on mechanistic variability, grounded in known physical and physiological limits of plant gas-exchange that are understood to be universal (Franks et al., 2014). This differs from empirical proxies, whose uncertainty representation is based on calibration error of modern-day observations without mechanistic constraints. Our canopy $C_a$ estimate ($445 \pm 618 / -100$ ppm, Fig. 2c) is independent of calibration error, based on universal gas-exchange mechanisms, and represents plant vegetative organs of multiple plant species that directly interacted with the available pool of atmospheric carbon dioxide. Previous $C_a$ estimates from the Oligocene/Miocene boundary based on boron isotopes and paleosol carbonates are generally lower than our estimates (Ji et al., 2018; Greenop et al., 2019) (Fig. 4b), whereas $C_a$ estimates based on stomatal index and recent alkenone-based $C_a$ estimates are more similar to our results (Kürschner et al., 2008; Super et al., 2018).

Reconstructions of globally elevated temperatures of 5–6 °C in the early Miocene (Hansen et al., 2013) with a $C_a$ of ~300 ppm (Ji et al., 2018; Greenop et al., 2019) upsets the expected ESS to $C_a$ during this period (Henrot et al., 2010). Geochemical $C_a$ proxy estimates consistently produce $C_a$ estimates that are too low to satisfy ESS to $C_a$ prior to the Pliocene (Royer, 2016) (Fig. 4a,b). Estimates from the fossil leaf-based stomatal index proxy for $C_a$ (Kürschner et al., 2008) on the other hand do indicate a positive correlation between temperature and $C_a$ in the Neogene (Fig. 4a). At present, there are too few studies that reconstruct $C_a$ using gas-exchange modeling to allow for a full comparison to other $C_a$ proxies; however,
our Ca estimates of ~450–550 ppm are in line with the ESS to Ca in the early Miocene (Fig. 4a,b), based on modelling experiments (Herold et al., 2010; Henrot et al., 2010). Moreover, thus far, Neogene Ca estimates reconstructed using gas-exchange methods (Reichgelt et al., 2016; Tesfamichael et al., 2017; Londoño et al., 2018; Moraweck et al., 2019) appear to agree with the suggested ESS to Ca (Fig. 4a,b).

Bulk organic and leaf wax δ^{13}C values reveal a ~4‰ decrease at Foulden Maar over a 10-meter interval at the beginning of Phase II (55–65 m depth), likely representing a time period of <10 kyr (Fox et al., 2016). This shift in isotopic composition suggests a substantial change in the global carbon cycle (Reichgelt et al., 2016). The mode of reconstructed values in this study suggests and increase of ~450 to 550 from Phase I to Phase II (Fig. 3). The Ca values stay near 550 ppm throughout Phase II and Phase IIIa, representing a 20–40 kyr time period (Fig. 3). Absolute dating of Foulden Maar based on paleomagnetic reversals in the core, annual lamination of lake sediments, and basalt-derived Ar/Ar dates indicates that the deposition of the Foulden Maar sediment coincided with the termination of the earliest Miocene (Mi-1) glaciation of Antarctica (Fox et al., 2015). Interestingly, an increase in Ca from ~450 to ~550 ppm at the termination of Mi-1 is consistent with modeling studies indicating that Ca > 500 ppm is necessary to terminate a large-scale Antarctic glaciation (DeConto et al., 2008). We note that with the current data available, it is not possible to exclude the possibility that modeled Ca changes in the record were influenced by canopy density changes or regional hydroclimate. However, our observations from Foulden Maar are inconsistent with hydrological, ecological or Ca changes as the sole driver of plant physiological response (Reichgelt et al., 2016), and it is more likely that two or more of these parameters changed in concert.

3.3 Elevated CO2 and the early Miocene biosphere

The Foulden Maar Miocene rainforest was primarily evergreen (Lee et al., 2016). The main Miocene canopy trees at Foulden Maar, *Litsea calicarioides*, *Cryptocarya taieriensis*, *C. maarensis*, cf. Elaeocarpaceae/Cunoniaceae and cf. Myrtaceae, had relatively high iWUE (Miocene iWUE first quartile [Q1] – third quartile [Q3] = 70–101) compared to modern evergreen trees (evergreen iWUE Q1–Q3 = 31–
Reconstructed iWUE from tropical early Miocene plants (Tesfamichael et al., 2017; Londoño et al., 2018) is slightly higher (Q1–Q3 = 80–125) (Fig. 5a). The difference between reconstructed Miocene iWUE and that of modern deciduous trees is greater still (deciduous iWUE Q1–Q3 = 27–52), consistent with the expectation that increased Ca favors evergreen trees (Niinemets et al., 2011; Soh et al., 2019). In the method of reconstruction used here, iWUE is ultimately an expression of leaf δ¹³C and conductance (see Methods section 2.3). Therefore, similar to reconstructed Ca, iWUE may be sensitive to environmental factors other than Ca. For example, leaf δ¹³C can change in response to edaphic conditions and precipitation (e.g. Kohn, 2016; Cornwell et al., 2018), as well as vapor pressure deficit (VPD) (Franks et al., 2013). The climate of Foulden Maar in the early Miocene was warm-temperate to subtropical, compared to the cool-temperate forests in southern New Zealand today (Reichgelt et al., 2019). Though reconstructed relative humidity at Foulden Maar is within the range of modern New Zealand forest biomes, the average monthly VPD was 500–700 Pa, compared to 250–450 Pa today (Fig. S3), which may result in a similar reconstructed iWUE as under elevated Ca (Franks et al., 2013). However, the reconstructed ecosystem at Foulden Maar is a broad-leaved humid rainforest (Bannister et al., 2012), which likely had a high annual moisture surplus (Reichgelt et al., 2019). Increased water-use efficiency in response to relatively high VPD compared to modern would only be a positive trade-off if water availability were limiting. Additionally, reconstructed iWUE from both temperate and tropical early Miocene floras are high compared to modern, suggesting a global signal, such as would be expected to globally elevated Ca; not from VPD as the early Miocene tropics would not be warmer than today (Herold et al., 2010). Most importantly, the modern iWUE data (Fig. 5a) are from a global database that includes environments with annual moisture deficits (Maire et al., 2015). Because reconstructed early Miocene iWUE is higher even than modern plants experiencing high VPD, we argue that VPD differences cannot explain the high iWUE values of the early Miocene, and that increased efficiency due to higher Ca is the best explanation.

In contrast to iWUE, reconstructed conductance to water (Gw) for Miocene trees is similar to the modern-day range at the same latitude (Fig. 5b), a somewhat surprising result because Gw is expected to
be reduced in high $C_a$ climates (Franks and Beerling, 2009). Studies on modern forests also suggest the absence of a reduction in $G_w$ to enhanced $C_a$ (Yang et al., 2016; Gimeno et al., 2018), or even an increase in the $G_w$ (Frank et al., 2015). A longer growing season together with increasing VPD was proposed to explain increasing $G_w$ in modern European forests (Frank et al., 2015). Similarly, a relatively high water flux from the forest to the atmosphere due to high water supply (Reichgelt et al., 2019) and high VPD (Fig. S3) could explain the broad similarity in the range of modern and early Miocene $G_w$, despite higher $C_a$. The early Miocene $G_w$ from tropical latitudes are within the range of modern evergreen tropical trees, though relatively low (Early Miocene Q1–Q3: 0.08–0.13 mol m$^{-2}$ s$^{-1}$, modern evergreen Q1–Q3: 0.07–0.2 mol m$^{-2}$ s$^{-1}$) (Fig. 5b).

A longer growing season likely resulted in the high total annual carbon flux ($A_{tot}$) to the biosphere reconstructed for Foulden Maar (Fig. 5c). Early Miocene trees at 50°S likely assimilated $A_{tot}$ Q1–Q3 = 265–696 gC m$^{-2}$ yr$^{-1}$, in comparison to $A_{tot}$ Q1–Q3 = 108–182 gC m$^{-2}$ yr$^{-1}$ in modern evergreen forests, and $A_{tot}$ Q1–Q3 = 249–410 gC m$^{-2}$ yr$^{-1}$ in modern deciduous forests at the same latitude (Fig. 5c). Early Miocene tropical trees appear to have slightly higher total annual carbon flux ($A_{tot}$ Q1–Q3 = 596–1220 gC m$^{-2}$ yr$^{-1}$) than today ($A_{tot}$ Q1–Q3 = 329–721 gC m$^{-2}$ yr$^{-1}$), which, with a year-round growing season in the early Miocene (like today), is likely attributable to a leaf-level fertilization effect, similar to what is observed in modern carbon fertilization experiments (Norby et al., 2003; Bader et al., 2013; Yang et al., 2016). Although this estimate cannot take the number of leaves per unit area into account, these results suggest enhanced leaf-level productivity during higher than modern $C_a$ in the early Miocene.

The methods used in this study provide an alternate approach to controlled carbon fertilization experiments, such as the Free Air Carbon Enrichment (FACE) experiments (e.g. Long et al., 2004), toward investigating the effect of increased $C_a$ on the biosphere. FACE experiments provide data on the physiological effects of carbon enrichment on species that evolved under, or had thousands of years to adapt to pre-industrial $C_a$ ($\approx$ 280 ppm), and the physiological changes detected in canopy species are measured as a direct response or over leaf generations (e.g. Norby et al., 2003; Yang et al., 2016). By contrast, our data provide an insight into species that evolved under higher than pre-industrial $C_a$ and had
many generations of individuals to adapt to incrementally slow changes. The direct, or multi-year physiological response of modern forest trees to enhanced $C_a$ is non-linear and non-uniform (e.g. Long et al., 2004; Ainsworth and Long, 2005), and therefore further investigations into the physiology of ancient plants operating in high-CO$_2$ worlds are needed to reveal the complexity of plant responses over evolutionary timescales.

4 Conclusions

Leaf-level gas-exchange derived $C_a$ estimates suggest that early Miocene atmospheric CO$_2$ was higher than pre-industrial levels at 450–550 ppm, further solidifying the growing consensus of relatively high early Miocene global temperatures maintained by high atmospheric CO$_2$ (Kürschner et al., 2009; Tesfamichael et al., 2017; Super et al., 2018; Londoño et al., 2018; Moraweck et al., 2019). A relatively high $C_a$ in the early Miocene also satisfies an Earth System Sensitivity of 3–7°C (Hansen et al., 2013; Royer, 2016). A potential shift in atmospheric CO$_2$ from 450 to 550, and back to 450, is recorded in the 100 kyr of sedimentation and leaf deposition at Foulden Maar. A disruption of the regional carbon and hydrological cycle was also recorded in leaf-wax $\delta^{13}C$ and $\delta D$ (Reichgelt et al., 2016), and may be linked to the Antarctic deglaciation at the termination of the Mi-1 (DeConto et al., 2008; Fox et al., 2015; Liebrand et al., 2017).

The first record is provided of increased Miocene leaf-level intrinsic water-use efficiency in both temperate New Zealand and the tropics, and we provide evidence for increased leaf-level productivity in temperate New Zealand. Enhanced productivity and water-use efficiency on other landmasses in temperate latitudes during the early Miocene, such as North America, Australia, and Asia, would have had a major impact on the global carbon and water cycles. Our gas-exchange results from New Zealand, supplemented with results from Ethiopia (Tesfamichael et al., 2017) and Panama (Londoño et al., 2018) provide empirical evidence for high water-use efficiency in the globally warmer world of the early Miocene, associated with elevated $C_a$. Tropical trees with high water-use efficiency compared to modern, would have likely facilitated forest survival in climates where currently tropical savannas and grasslands...
exist. These high water-use efficiency forests in the tropics likely persisted until the late Miocene when reduced $C_a$ (Mejía et al., 2017) started favoring the expansion of grasslands, in particular grasslands with the $C_4$ pathway that is more efficient under low $C_a$ and high temperatures (Strömberg, 2011; Polissar et al., 2016).

Emission scenarios suggest that atmospheric CO$_2$ will reach our reconstructed early Miocene values of 450 ppm by 2030–2040 CE. While the global temperature response may lag the $C_a$ increase, and forest habitat expansion is hampered by the slow dispersal and growth rate of climax forest trees and anthropogenic influence (e.g., forest fragmentation and fire), early Miocene water-use efficiency and productivity estimates provide insight into future-biosphere potential, as well as into selective pressures that influence the types of plants that may proliferate under future elevated $C_a$.

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Author contributions. TR and WJD conceived of the idea and performed data analyses. BRSF and DEL collected sediment core, BRSF and TR sampled the sediment core, JGC and JMB identified fossil leaf taxa. ACVM and TR gathered data from fossil leaves. TR and WJD wrote the paper and all authors contributed to the final manuscript.

Competing interests. The authors declare no competing interests.
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Figure 1. Foulden Maar site information. (a) Location of the Foulden Maar deposit and paleogeographic reconstruction of early Miocene New Zealand (Boyden et al., 2011; Lee et al., 2014). (b) Schematic reconstruction of the Foulden Maar depositional environment. (c) Stratigraphic column of the Foulden Maar core (Fox et al., 2015), with sample locations and bulk organic δ$^{13}$C (Reichgelt et al., 2016).
Figure 2. Foulden Maar paleoecology and atmospheric CO$_2$ reconstructions. (a) $\delta^{13}$C values and stomatal density (error bars representing ±1σ) from the fossil leaves of Foulden Maar provide constraints to distinguish canopy leaf types from understory, because understory leaves tend to have a high range of $\delta^{13}$C and low cell density (Graham et al., 2014; Bush et al., 2017). (b) Paleoecological reconstruction of the dense rainforest at Foulden Maar with a canopy comprising *Litsea calicarioides* (Lcal), *Cryptocarya taieriensis* (Ctai), *C. maarensis* (Cmaa), cf. Elaeocarpaceae/Cunoniaceae (E/C), and cf. Myrtaceae (Myrt), and an understory comprising cf. *Myrsine* (Myrs), cf. *Ripogonum* (Rip), cf. *Dysoxylum*
(Dys), and leaf type “O”. *Hedycarya pluvisilva* (Hplu), *Laurelia otagoensis* (Lota), *Beilschmiedia otagoensis* (Bota), cf. *Cryptocarya* (cfC), cf. *Endiandra* (cfE), and leaf types “C”, “H”, “P”, and “Q” could not be ecologically placed with certainty. (e) Probability density distributions of $C_a$ reconstructions from canopy (thick light green line) and understory components (thick dark green line) using a gas-exchange model (Franks et al., 2014). Grey curves represents the probability distribution of 10,000 Monte Carlo reconstructions on a single fossil leaf.

**Figure 3.** Probability density distributions of $C_a$ reconstructions using a gas-exchange model (Franks et al., 2014), divided by bulk carbon isotope phases (Fig. 1c).

Fig. 4
Figure 4. Neogene Earth System Sensitivity (ESS) and $C_a$ reconstructions. Calculated $C_a$ levels for an ESS range of 3–7 °C (orange shaded area) for the last 30 Ma (a), and for the interval between 22.5–23.5 Ma (b), the red dashed line in (b) indicates the global average surface temperature ($T_s$) in the earliest Miocene (Hansen et al., 2013). The ESS envelope was determined using deep-sea $\delta^{18}O$ of benthic foraminifera (Zachos et al., 2001) and the transform function approach from Hansen et al. (2013) (Supplementary Information). Proxy-based Neogene $C_a$ reconstructions are derived from a previously published compilation (Foster et al., 2017) and are supplemented with more recently published data (Ji et al., 2019; Londoño et al., 2018; Super et al., 2018; Greenop et al., 2019; Moraweck et al., 2019, Steinthorsdottir et al., 2019). Error bars on gas-exchange based proxy estimates represent ±1σ.
Figure 5. Early Miocene leaf-level physiological parameters of canopy trees. (a) Intrinsic water-use efficiency (iWUE) of evergreen (green circles) and deciduous trees (red circles) based on modern leaf-level measurements (Maire et al., 2015), and fossil reconstructions (green triangles and diamonds). Error bars on fossil-derived data indicate ±1σ, box-and-whisker plots indicate median, first and third quartile (Q1 and Q3), and 95% confidence interval of modern leaves of canopy trees. Individual datapoints are randomized on the x-axis for a clearer depiction of the distribution. (b) Conductance to water (Gw) from modern evergreen (Ev) and deciduous (Dec) trees (Maire et al., 2015) and fossils (EM) from different latitudes. The shaded red and green areas indicate the Q1–Q3 range of modern evergreen and deciduous trees, respectively, and the dashed lines indicate the overall linear trend with latitude. Text in panel is the Q1–Q3 range for each group, grouped in 5° latitude bins. (c) Total annual carbon flux per unit leaf area (Atot) from modern evergreen (Ev) and deciduous (Dec) trees (Maire et al., 2015) and fossils (EM) from different latitudes. The shaded red and green areas indicate the Q1–Q3 range of modern evergreen and deciduous trees, respectively, and the dashed lines indicate the overall exponential trend with latitude. Text in panel is the Q1–Q3 range for each group, grouped in 5° latitude bins.

Data availability. All raw measurement data on fossil leaves generated for this paper is available in the online supplementary information. Raw measurements on fossil leaves from Ethiopia (Tessamichael et al., 2017) and Panama (Londoño et al., 2018), δ18O measurements (Zachos et al., 2001), and iWUE, Gw
and $A_n$ measurements on modern plants (Maire et al., 2015) are available through the cited original works.